ON THE ORIGIN AND THE CAUSATION OF VITAL MOVEMENT.[1]

I.

AMONG the phenomena of life the movement of masses, or mechanical work, takes a prominent place. It is the most accessible of all the vital processes to our sensual perceptions, so universally distributed, and so bound up with most of the activities of organisms that it might almost be designated the incarnation of life.

In saying this it must be understood that vital movement is by no means exclusively confined to animals—that it is not, as was once believed, a special animal function; on the contrary, it is an attribute of *all* living matter, as well of the lowest creatures as of the most highly developed plants, so that, however extraordinary it may appear, the activity of our muscles which enables us to transform sensation into action finds an analogue in the plant. Our conviction of the inter-connection and profound unity of all living things has thus a physiological foundation, based as it is not merely on the community of derivation and of structure of living things, but also on the proof of similar activities.

If a division of the morphological from the physiological is in any way permissible, it may be said that the unitary conception of life for which our age is distinguished rests in a higher degree on the knowledge of vital *processes* than is commonly recognized, and in fact is just as much founded on physiological experience as on that of the *forms* of the organism.

From the traditional conception of life, which scarcely contained more than that everything between life and death is the antithesis of the not living, it is a long road we have had to travel to attain to the modern conception of the *real* unity of life; and a remarkable road, since it bears witness to the confident anticipation of victory, in face of all impediments raised up by science itself. Movement, and nothing less, had been placed at the summit of that antithesis, which physico-chemical research in the animal and vegetable kingdom had revived with the discovery that the plant transformed kinetic into potential energy, and the animal the latter into the former. While the animal made use of oxygen to generate heat and perform work through the metabolism of its substance, the plant made use of the heat in reducing and synthetic processes for the accumulation of potential energy in the form of its own consumable substance and the expired oxygen.

With whatever unassailable correctness this conception comprehends life as a whole, affording a pleasing solution of its antithesis by referring animal activities to nourishment by the plant, the latter to the products of the combustion of the animal body, and both in the last instance to the forces of the sun as original source of all life, yet *this* did but cast up the sum-total of the processes of life, and did but express more intimately than before that which divides the most highly-developed branches of the animal and vegetable kingdom, in which the divergence of forms and arrangements is greatest. For *by the side of* this distinction there exists even between man and the most highly elaborated plant a connection of a kind quite other than the symbiotic interdependence through the medium of light, air, and food, a community, however, which is not disclosed until we go back to the ultimate elements of organization.

As in the animal synthetic processes are not wanting, without which it could not even produce a molecule of the colouring matter of its blood, so in the plant we are acquainted with dissociations and combustion, and also with evolution of heat and movement of masses; not that by this I refer to those coarser movements which are referable to turgescence, but primitive movements, which we find first in the smallest elementary organisms, of which all living beings are made up.

We have almost in our own persons lived to see the old anticipation of a single kingdom of living things become gradually an established truth through the discovery of the cell. After the ground-lines of the construction of plants and animals out of originally similar *nucleated* cells had been established by Th. Schwann, and since Darwin's immortal work enabled us to derive everything that ever lived or will live from one single cell, we have come to realize that every single organism renews in itself the work of past ages, and again builds itself up from a germ similar to that from which its most ancient ancestors started.

This conviction has become so firmly implanted in our generation that now we scarcely feel the gaps which still exist in our actual knowledge, and almost unjustly under-estimate that which the investigations of our contemporaries yet add to the cell-theory, as if it were mere work of repetition. And yet it has been very extensive and decisive—for example, the recent researches upon the intimate structure of the cell-nucleus—since nothing less results from it than that the reproduction of the cell by fission takes place identically, down to the most minute details, in all animals and plants.[1]

Now, if the *shaping* of the cell and all the *fashioning* of forms is an *activity*, and if Morphology, "since it has made the *arising* of form more its study than the describing of what is already completed," has become part of Physiology, it might be possible and conceivable that research directed to *all* activities and going beyond the *visible* form to the chemical components of the structures and the transformation of substance and force, should observe great differences in processes where all our morphological experience would only have shown identity. We were near enough to this point; for if it were true, as was long assumed, that that which is the bearer and the seat of the most essential of all vital processes *in* the cell is completely formless, it is not easy to see why the form should be so determinant of function.

We have hope that this is not so, and will endeavour to show in Movement the functional as well as the morphological unity of all living matter.

As I have already said, there is an elementary kind of movement in the cell, carried out by the cell-body—that part of the cell which, in contradistinction to nucleus, membranes, and various inclosures, has been designated protoplasm. The protoplasm moves itself, as in the case of certain free-living Protozoa, like the long-known Amœba, like the so-called sarcode—in many cases better comparable to the movement of the pseudopodia of Rhizopods. The resemblance of the latter to what was formerly called the sap-current in many plant-cells, led Ferd. Cohn[2] to interpret plant protoplasm as sarcode, an idea actively supported by Max Schultze,[3] the best authority on pseudopodial movement. It is not necessary to say here how widespread protoplasmic movement is, for there cannot be a cell that does not present it at some stage of its existence. Doubt on this subject can only exist in regard to the smallest of all organisms, those of fermentation, of putrefaction, and of pathogenic activity which are too small for observation. But even in these, from the movement they perform as a whole, we have grounds to infer the existence of a protoplasm.

It is proved that protoplasmic movement does not follow external impulses or currents, but is a spontaneous activity. It may go on in opposition to gravity, and overcomes frictional resistance, as shown by the mass itself moving forward on surfaces of every kind, and being able to drag heavy bodies along with it. It is proper mechanical work.

The cause of the movement can only be an internal one, residing in the contractile substance itself, and can only consist of chemical processes taking place within the peculiar pasty, slime-like mass. Yet the question had to be put whether these processes were not first set up by something coming perhaps from the outside, for the movement changes, sometimes stops or takes place more slowly, or occurs but partially, and may by many means be artificially aroused or diminished.

At this point experimental physiological research had to step in, attacking the problem in the same way as it had long before done in the case of the most highly-developed contractile structures, the muscles. A muscle behaves so far just like protoplasm that its contraction does work, which can only depend on chemical transformations of its own substance, during which potential is converted into kinetic energy; but it differs in that a distinct impulse from without is needed to set the game going. In normal conditions it receives the initiating impulse from its nerve, and nothing else appears able to take its place, since nothing that might otherwise act upon it, such as the motion of the blood or changes in its constitution, disturbs its repose. But if we let electric currents traverse the muscle, or if we suddenly change its temperature, or act upon it mechanically or chemically, contractions result which do an amount of work out of all relation to the insignificant impulse; the means employed only set going the process peculiar to the muscle; and this is what is meant when we term them *stimuli*, and the faculty of muscles to react to them irritability.

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[1] "On the Origin and the Causation of Vital Movement (*Ueber die Entstehung der vitalen Bewegung*)," being the Croonian Lecture delivered in the Theatre of the Royal Institution on May 28, 1888, by Dr. W. Kühne, Professor of Physiology in the University of Heidelberg.

[1] The most complete exposition of these important later discoveries on the reproduction of the cell is to be found in the book of W. Flemming, "Zellsubstanz. Kern und Zelltheilung," Leipzig, 1882. Cf. the "Kurze historische Uebersicht" (p. 385), with the quotations from the works of Schneider, Strassburger, Bütschli, Flemming, O. Hertwig, and the researches of Auerbach, Balbiani, van Beneden, Eberth, Schleicher, Balfour, and others.

[2] "Nachträge zur Naturgeschichte des Protococcus pluviatilis," *Nova Acta Acad. Leopold. Cæsar.*, vol. xxii. Part 2, p. 605 (1850).

[3] "Ueber den Organismus der Polythalamien," Leipzig, 1854.

Now, is protoplasm irritable in this sense? Experiments on objects of every kind have answered this affirmatively, and, more than that, have even shown a striking agreement with the irritability of muscle. Of the above-mentioned agents, besides rise of temperature, which ultimately sets all contractile cell-substance in maximal contraction—a heat tetanus[1] which disappears with cooling—the electric current has shown itself the most efficient, the stimulus which most surely excites muscles of every kind as well as all nervous matter, and has thence become the most indispensable instrument of physiology.

I may be permitted to adduce an example because it illustrates what is typical and essential.[2] It is the case of the fresh-water Amœbæ. Every time these organisms, moving like melting and rolling drops, are subjected to an induction shock, they contract almost to a sphere, and assume the spherical form completely if the shocks follow each other at short intervals, being by this means fixed for a longer time in this condition. Feebler shocks, which singly have no effect, become effective by summation when applied in quick succession, just as in the case of muscle. If the movements of the animal by itself are sluggish, on electrical stimulation they are strengthened and accelerated. Thus the stimulation increases the natural movement, and if increased stimulation brings about repose, it is only the apparent repose of prolonged maximal contraction, like that of our muscles when we hold out a weight for some time at arm's length. All protoplasm behaves in this way from whatever source derived. Larger masses which cannot contract to one sphere (as in many plant-cells, or those great cake-like giant masses of the plasmodium of the Myxomycetes) form several such spheres in part connected by thread-like bridges. Everywhere the taking on of a figure with smallest surface is the result of stimulation and the expression of augmented contraction.[3] That which was outstretched becomes shorter and in like measure thicker, just as a muscle swells when it shortens itself.

Since protoplasm, which either does not move at all spontaneously or so slowly that we cannot perceive it, reacts in the same way to stimuli, we must in the case of ordinary movements infer the existence of processes originating them either in the interior, *i.e.* automatic stimuli, or of external processes which had at first escaped us. Whoever sees for the first time the action of any one of the simpler independent Protozoa cannot avoid the idea that psychic activity in the strictest sense of the term lies behind it, something like will and design. He sees the elementary being seeking and taking up food, avoiding obstacles, and when touched by foreign objects energetically drawing back, so that he infers sensation also. Possibly he has struck the correct solution—at least we could not refute him—but we should put his deduction to a hard proof if we showed him the same phenomena in the colourless cells of his own blood, or in the protoplasm of a plant-cell; and if we placed him before the rhythmically contracting cells from the beating heart of a bird's egg incubated barely a couple of days, he would certainly wish with us that the search were for a more material cause, and hope that among them some chemical or physical cause might be found to set up the process. Biology cannot indeed yet claim to have established such causes in explanation of the automatism of protoplasm, but no one will blame the science for continuing the search for them.

Some causes are already excluded, *e.g.* light, although there are a few micro-organisms whose movements are excited by it.[4] Fluctuations of temperature may also be left out of account. On the other hand, oxygen has a notable influence.[5] Withdrawal of the vital air stops all protoplasmic movement, though without killing the cell-body, as is seen from the fact that after the loss of automatism electrical stimulation can supply its place, and that the normal movements return on readmitting the air.

We might thus consider oxygen the prime mover in automatism, and processes of oxidation its essence, did we not remember that many objects need very prolonged withdrawal of the gas to come completely to rest. This might, however, depend upon the difficulty of removing the last traces of oxygen completely, or it may be that these cannot be removed by the means adopted, but must remain until consumed by the protoplasm itself.

Since protoplasm is of pap-like softness, and may be in a state of rest or motion at any spot, its exterior limits are just as capable of change as everything within it is capable of quitting its position and taking up any other. Thus the movement cannot become more ordered until obstacles confine and direct it. Between the perfected organization of contractile substance in muscle and that of protoplasm capable only of unordered movement, we meet a succession of significant steps by means of which we can see how the ordering was attained. The first step would seem to consist in the uncommonly widespread flagellar and ciliary motion, in which an elastic structure, affixed on one side to the contractile mass, is drawn down or bent by its movement, straightening out again in the rhythmic pauses of repose. A further step, at which the contraction can only take place along an axis, consists in the arrangement of the protoplasm in fine strips wholly or partially surrounded by elastic walls, or again in elastic fibrils being embedded in protoplasmic processes. In this case we have actual primitive muscles before us, of which the most elegant examples are known in the Infusoria among the Vorticellæ and Stentores. The movement of these structures is quite like that of muscle. The strips lengthen and thicken, and they may also be contracted in quick twitches or in a prolonged tetanus, the relaxing, like the stage of diminishing energy of all muscles, always proceeding more slowly than that of the increasing energy *before* the maximum.

The muscles of the unicellular Infusoria, no longer doubtful in a physiological sense, show us muscle as a constituent of the cell, and differentiation, without the production of new cells specially endowed for the purpose, taking place in *one* cell to the extent of elaborating contractile elements determinate in form and precise in work. It is very noteworthy that side by side with these muscular strips provided with highly regulated movement, other protoplasm persists, which continues uninterruptedly its ordinary unordered movements, while no such unrest is to be remarked in the muscles. On the contrary, these latter are only used from time to time, apparently for attaining distinct objects. We get the impression that the automatism has, as it were, been lost by this portion, so that it must wait for stimuli to reach it from other parts of the cell. If oxygen really applies the first spur to the protoplasm, it has no direct power over the primitive muscle, so that compared with the protoplasm the muscle is endowed with a diminished irritability.

It has often been said that protoplasm presents the complete set of vital phenomena—assimilation, dissimilation, contractility, automatism, resorption, respiration, and secretion, and even reproduction by dividing. Leaving reproduction on one side, as now disputed, and on good grounds, we can assent to the assertion, and examine which of those functions remain for the products of differentiation. In the case of the muscle, we find it to be all of them with the exception of a single one; for, while it undoubtedly takes part in nutrition as in respiration and carries on a chemical exchange, all of which are indispensable for contractility, *i.e.* for its work, and since secretion generalized signifies merely the throwing off of broken-down products, it is wanting *only* in automatism, that faculty of reacting to certain stimuli, which remained reserved for protoplasm. In this there is nothing opposed to the assumption that protoplasm as opposed to muscle possesses elementary *nervous* properties.

The above is sufficient to show the transition to the very highly developed motor apparatus which distinguishes the animal kingdom from almost its lowest stages—I mean the bi-cellular apparatus, which consists of separate cells united only for *one* purpose, one of which presents the exciting nerve, the other the obedient muscle.

From past experience we know that division of the nerve, or, more correctly speaking, removal of the nervous cell substance, condemns the muscle to rest. The stimuli then start from the nerve-cell, to them the muscles react by doing work, and they are conveyed to the muscles through the continuation of the cell which the nerve-*fibre* presents. We need not yet trouble ourselves how the excitation of the nerve-cell arises, whether through external—sensory—stimuli, or through an enigmatical psychic act, or through chemical influences; certain it is that these were, before the division of the nerve, the sole impulse to the muscle's movements. But what the muscles lack we can supply artificially, and more; we can put the nerve-remnant in such manifold states of excitement as it never before experienced from its cell-body, so that the muscle is compelled to undergo many kinds of movement quite new to it, and we can attain the same result by direct stimulation of the muscle.

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[1] W. Kühne, "Untersuchungen über das Protoplasma und die Contraktilität," Leipzig, 1864, pp. 42, 66, 87, 102.

[2] Kühne, *ibid.* p. 30.

[3] Th. W. Engelmann, five years later, confirmed the passage of protoplasm, especially of Amœba, to the spherical form on stimulating; cf. his "Beiträge zur Physiologie des Protoplasmas," *Pflüger Archiv*, vol. ii. 1869, p. 315, and "Handbuch der Physiologie, herausg. von L. Hermann," vol. i. p. 367.

[4] Engelmann, "Ueber die Reizung des contraktilen Protoplasma durch plötzliche Beleuchtung," *Pflüger Archiv*, vol. xix. p. 1.

[5] Kühne, *l.c.*, pp. 50, 67, 88–89, 104–106. The cessation of the so-called sap-stream in the cells of *Chara* on excluding the air by oil was observed as far back as 1774 by Bonaventura Corti; and further by Hofmeister in *Nitella* under the influence of reduced atmospheric pressure. Cf. Engelmann in "Handbuch der Physiol. von Hermann," vol. i. Part 1, p. 362.

In the circle of these experiences arose the controversy, not yet quite ended,[1] as to muscular irritability; properly, the question whether it was, in general, possible to stimulate anything artificially that is not nerve—that is, to set free the activity peculiar to a non-nervous structure by the means at our command.

Haller, who was the first to occupy himself minutely with the stimulation of muscle, and introduced the term irritability, decided, but only incidentally and by the way, that the stimulus could strike also the ramifications of the nerve in the muscle, and he was far from interesting himself in the question in the modern sense, or from suspecting the point of view from which the independent irritability of muscle would later on be questioned. We ought not to blame him much for the latter, since even to-day it is not easy to understand the motives of an opposition now continued for more than a century. At the outset, if I am not mistaken, the teaching of the Animistic, or, as it might now be called, the Neuristic school, led to the conception that not only the excitation and regulation of the various functions, but the actual endowment of the several tissues with their respective activities, was the work of that everywhere predominant and distinctly animal contrivance, the nervous system.

In connection with this, there seems to have arisen the view of the ubiquity of nerves—that is, of so fine a penetration of the parts with nerve radiations, that, especially in muscle, not the smallest particle free from nerve could be demonstrated, a view which, on the strength of microscopic research, is coming up again at the present day in a constantly new dress, and finds energetic adherents,[2] but, as we shall see, to be refuted, especially by experiment. If we disregard this, we shall find the tendency to consider only nerves as excitable, in some degree founded on the differentiation which transferred automatism to the nervous matter, robbing all the remaining tissues of irritability, so that they only retained the faculty of reacting to the stimulated nerve with which they were bound up. This was as much as saying it was impossible artificially to replace the nervous stimulus, or that, if we did succeed, we were strictly imitating it, in which case, indeed, we should have come unawares upon the solution of the problem of motor innervation. Against such arguments it availed nothing to point out the excitability of nerveless sarcode, as was often done in favour of irritability; for, just as it was formerly useless, because the real genetic connection of sarcode and muscle was not known, so to-day it would have to be rejected, because automatic protoplasm can also be correctly considered nervous.

A non-irritable muscle would strike us as strange enough, and, against all expectation, different from the nerve, when we consider that the nerve-fibre, although incapable of being affected by all the natural stimuli which excite its ganglion-cells, free, that is, from automatism, is artificially excitable at every spot by the most different agents. However, we have no further need of such considerations, since the question of irritability lies within a region where, instead of speculation, observation and experiment have become decisive.

As a matter of fact, the older statements, long considered a good basis for opposing irritability, are incorrect, as, for instance, that an excised piece of muscle in which no nerves could be seen with the lens did not twitch on stimulating it.

We can show you a little piece, 3 millimetres long, from the end of the sartorius muscle of the frog, in which the best microscope discovers no traces of nerves, easily made recognizable by osmium-gold staining (Fig. 1). Such a piece, transversely cut off, twitches, as we know, at each effective muscular stimulus. Pieces which can be obtained free from nerves from many other muscles behave in the same way, as, for instance, pieces from the delicate muscles of the pectoral skin of a frog (Fig. 2).

Further, the assertion was incorrect that everything that excited the nerve made the muscle twitch, and *vice versâ*; for we see here a sartorius suspended in ammonia vapour, contracting powerfully, while a nerve entirely submerged in liquid ammonia appears wholly unstimulated, for it does not rouse the thigh muscles from their repose.

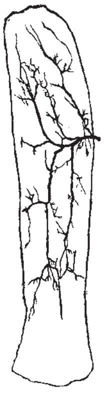

FIG. 1.[1]

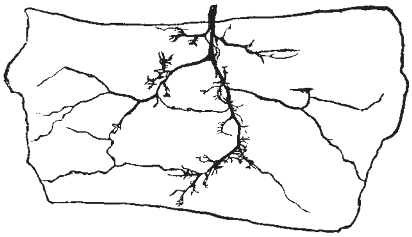

FIG. 2.

Conversely, we see a thigh whose nerve dips into glycerine in maximal contraction, and, on the other hand, a muscle in contact at its excitable end with the same glycerine remains at rest, yet it twitches if I dip it in up to its nerve-bearing tracts.[2]

These are old experiments,[3] and it is admitted they have overthrown the earlier opinion. But they have not been deemed sufficient to prove muscular irritability, because the ultimate endings of the nerves might have an irritability other than that of their stems. This is the only objection still raised. One could wish no other were conceivable, for this one admits of refutation.

(*To be continued.*)

THE HEMENWAY EXPEDITION IN ARIZONA.[4]

DR. JACOB L. WORTMAN, of the United States Army Medical Museum, has just returned from Arizona, where he has spent the winter and spring attached to the Hemenway South-Western Archæological Expedition under the direction of Frank Hamilton Cushing, which was mentioned in the March number of the *Naturalist*, and he confirms the importance as well as the genuineness of the discoveries of Mr. Cushing. The Expedition is thoroughly equipped and well organized, and its investigations have been conducted in a vigorous and scientific manner, with special reference to the many details which go to make collections of this character of value to the scientific student. Not only have the ruins been carefully surveyed and mapped, but each specimen has been labelled with great care, in

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[1] Cf. J. Rosenthal, "Allgemeine Physiologie der Muskeln und Nerven," Leipzig, 1877, p. 255.

[2] J. Gerlach, "Ueber des Verhalten der Nerven in den quergestreiften Muskelfäden der Wirbelthiere," *Erlangen Phys. Med. Soc. Sitzber.*, 1873. "Das Verhältniss der Nerven zu den willkürlichen Muskeln der Wirbelthiere," Leipzig, 1874. "Ueber das Verhältniss der nervösen und contraktilen Substanz der quergestreiften Muskels," *Archiv Mikrosk. Anat.*, vol. xiii. p. 399. A. Foettinger, "Sur les terminaisons des nerfs dans les muscles des insectes," *Archives de Biol.*, vol. i., 1880. Engelmann, *Pflüger Archiv*, vol. vii, 1873, p. 47; vol. xi., 1875, p. 463; vol. xxvi. p. 531. In these publications it is sought to prove that the motor nerves pass either into the interstitial nucleated substance of the muscle (therefore into the sarcoglia) or into the layers of the "Nebenscheiben." This latter view is opposed by, among others, A. Rollett, in his thoroughgoing exposition of the structure of muscle (Vienna, *Denkschriften der k. Akad.*, vol. xlix. p. 29), and W. Kühne (*Zeitschr. f. Biol.*, vol. xxiii. p. 1.

[1] The drawings, Figs. 1, 2, 3, 5, 8, are taken from the papers of Dr. K. Mays, "Histophysiologische Untersuchungen über die Verbreitung der Nerven in den Muskeln" (*Zeitschr. Biol.*, vol. xx. p. 449), and "Ueber Nervenfasertheilungen in den Nervenstämmen der Froschmuskeln" (*Zeitschr. Biol.*, vol. xxii. p. 354); Figs. 9–13 are from the author's papers in *Zeitschr. Biol.*, vol. xxiii. pp. 1–148, Plates A–Q.

[2] The experiments were performed during the lecture by projecting on the wall images of the preparations enlarged some thirty times.

[3] Kühne, "Ueber direkte und indirekte Muskelreizung mittelst chemischer Agentien," *Müller's Archiv. f Anat.*, 1859, p. 213.

[4] Reprinted from the *American Naturalist*, June 1888. The writer is Mr. Thomas Wilson, of the Smithsonian Institution.